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A stage structured mosquito model incorporating effects of precipitation and daily temperature fluctuations

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Abstract

An outbreak of dengue fever in Guangdong province in 2014 was the most serious outbreak ever recorded in China. Given the known positive correlation between the abundance of mosquitoes and the number of dengue fever cases, a stage structured mosquito model was developed to investigate the cause of the large abundance of mosquitoes in 2014 and its implications for outbreaks of the disease. Data on the Breteau index (number of containers positive for larvae per 100 premises investigated), temperature and precipitation were used for model fitting. The egg laying rate, the development rate and the mortality rates of immatures and adults were obtained from the estimated parameters. Moreover, effects of daily fluctuations of temperature on these parameters were obtained and the effects of temperature and precipitation were analyzed by simulations. Our results indicated that the abundance of mosquitoes depended not only on the total annual precipitation but also on the distribution of the precipitation. The daily mean temperature had a nonlinear relationship with the abundance of mosquitoes, and large diurnal temperature differences can reduce the abundance of mosquitoes. In addition, effects of increasing precipitation and temperature were interdependent . Our findings suggest that the large abundance of mosquitoes in 2014 was mainly caused by the distribution of the precipitation. In the perspective of mosquito

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control, our results reveal that it is better to clear water early and spray insecticide between April and August in case of limited resources.

Keywords: Vector-borne disease; Intervention; Climate factors; Breteau index; Mathematical modeling

1. Introduction

In April 2015, a widespread outbreak of Zika virus disease began in Brazil and has spread to many other countries in South America, Central America, the Caribbean and Mexico. In Brazil, by the end of 2015, the Brazilian Ministry of Health estimated that 500,000-1.5 million people have been infected by the Zika virus (Paploski et al., 2016), which is a mosquito-borne virus transmitted by *Aedes aegypti* and *A. albopictus*, which also transmit other vector-borne diseases such as dengue fever and yellow fever, while species of *Anopheles* are the principal vectors of malaria and *Culex* species transmit West Nile virus and other infections. According to reports of the World Health Organization (WHO), more than 2.5 billion people in over 100 countries, approximately one third of the world's population, are at risk of contracting dengue alone and malaria causes more than 438,000 deaths every year globally, according to the 2015World Malaria Report (http://www.who.int/malaria/publications/worldmalaria- report-2015/en/).

As a main mosquito-borne disease, dengue fever can cause a severe flu-like illness and sometimes causes a potentially lethal complication. It was first recognized in the 1950s in the Philippines and Thailand and now up to 50-100 million infections are estimated to occur annually in over 100 endemic countries. In China, epidemics of dengue fever were first reported before 1940 (Qiu et al., 1993). In 1978, a sudden outbreak of dengue fever occurred in Foshan city of Guangdong Province (Qiu et al., 1993) and it spread to seven adjacent counties and cities where a total of 22,122 cases, including 16 fatalities, were reported (Guang et al., 2000). Since then outbreaks of dengue fever have occurred frequently in southern China. The outbreak of dengue fever in Guangdong province in 2014 has been the most serious outbreak in China so far.

Mosquito-borne diseases are sensitive to climatic factors. Several studies have been carried out on the correlation between mosquito-borne diseases and climate using statistical methods and they showed significant associations between climatic variables and disease incidence (Nagao et al., 2003; Depradine et al., 2004; Hsieh et al., 2009; Do et al., 2014). Wu et al. found a negative association of dengue incidence with temperature and relative humidity by using autoregressive models (Wu et al., 2007). (Eastin et al., 2014) revealed that dengue cases increase a few weeks after the daily temperature range remains within the temperature range optimal for mosquito survival and transmission of the disease (Eastin et al., 2014). In a study of an epidemic in Guangzhou, China, correlation analysis and time series analysis of climate data and dengue fever cases showed a positive correlation between dengue incidence and minimum and maximum temperatures, precipitation and humidities, and seasonal fluctuations in immature densities of *Aedes albopictus*, which were consistent with the dengue seasonality (Lu et al., 2009; Luo et al., 2012). These results indicate that climatic factors have a complex relationship with mosquito-borne disease transmission and so research on the effects of climate factors on the abundance of mosquitoes and on the transmission of mosquito-borne diseases is important.

Other studies have focused on mathematical models to investigate the epidemiology of mosquito-borne diseases by incorporating climatic factors into models. Some of these mathematical models are stage structured mosquito models considering the population dynamics of mosquitoes and climatic factors are incorporated into the reproduction, development and survival rates (Erickson et al., 2010; Beck-Johnson et al., 2013; Jia et al., 2016). For example, (Gong et al., 2011) established a climate-based model for West Nile *Culex* mosquito vectors in 2011. The model was validated with field data and the simulated abundance was highly correlated with actual mosquito numbers. Other mathematical models of disease dynamics are Susceptible-Exposed- Infectious-Recovered(SEIR) models, with or without considering vectors (Feng et al., 1997; Esteva et al., 2001; Derouich et al., 2006). Most of these models focus on the basic reproduction number, examine force of infection or transmission dynamics (Marques et al., 1990; Favier et al., 2006; Chowell et al., 2007; Wearing et al., 2006) and climatic factors are incorporated into the transmission parameters or with a statistical model. These papers usually focus on the sensitivity of the dynamics of mosquito populations or disease transmission to climatic factors, and on seasonal trends of the abundance of mosquitoes or disease outbreaks(Nago et al., 2007; Thammapalo et al., 2008; Li et al., 1985; Sanchez et al., 2006). Effects of the within- and between year spatio-temporal distributions of temperature and precipitation are rarely discussed. Besides, the effect of temperature is usually investigated under constant temperature conditions, namely the daily mean temperature. However, daily temperature fluctuations have shown to be important biologically (Carrington et al., 2013) and some studies have been published to investigate effects of daily fluctuations of temperature on the transmission parameters (Lambrechts et al., 2011; Liu-Helmersson et al., 2014). Therefore, in this paper, we mainly pay attention to a mosquito population model in relation to temperature and precipitation, which incorporates daily fluctuations of temperature. Based on previous research results and the dengue fever situation in Guangzhou in 2014, the objectives of this study were to improve knowledge of the relationships between climate and mosquito abundance, to explain the climatic reasons for the substantial outbreak of dengue fever in 2014 and to predict the effectiveness of potential control measures.

2. Methods

2.1. Model description

The life cycle of mosquitoes is composed of four distinct stages, including egg, larva, pupa and adult. The first three stages egg, larva and pupa are aquatic and defined as immature. So, our model was developed to encompass both immature and adult stages and is derived from a study of climate-based models for West Nile virus *Culex* mosquito vectors (Gong et al., 2011). Let M_{IM} be the number of immatures; M_A be the number of adults; W be the moisture index. The model is as follows:

$$\begin{cases} \frac{dM_{IM}}{dt} = b(t)M_A - d(t)M_{IM} - \mu_1(t)M_{IM} \\ \frac{dM_A}{dt} = d(t)pM_{IM} - \mu_2(t)M_A \\ \frac{dW}{dt} = \lambda(t) - \delta W \end{cases} \tag{1}$$

where $b(t)$ is the egg laying rate at time t; $d(t)$ is the development rate at time t; $\mu_1(t)$ and $\mu_2(t)$ are the mortality rates of immatures and adults at time t (as shown in Table 1); $\lambda(t)$ is the precipitation, and δ is the evaporation rate. As temperature has a major effect on insect development, the egg laying, development and mortality rates are considered to be temperature dependent. The form of these temperature dependent parameters were derived from (Gong et al., 2011), based on development results from laboratory studies. The explicit expressions for these parameters are as follows:

$$b(t) = b_0 + \frac{E_{\max}}{1 + \exp(-\frac{W(t) - E_{mean}}{E_{var}})},$$

$$d(t) = A\frac{T(t) + K}{298.15} \frac{\exp(\frac{HA}{1.987}(\frac{1}{298.15} - \frac{1}{T(t)+K}))}{1 + \exp(\frac{HH}{1.987}(\frac{1}{TH} - \frac{1}{T(t)+K}))},$$

$$\mu_1(t) = 1 - \mu_{01}\exp(-\frac{T(t) - T_{01}}{v_1})^2,$$

$$\mu_2(t) = 1 - \mu_{02}\exp(-\frac{T(t) - T_{02}}{v_2})^2,$$

where b_0 is the baseline egg laying rate; $E_{\max}$ is the maximum egg laying rate above the baseline; E_{mean} is the value at which the moisture index produces 50% of $E_{\max}$ and E_{var} is the variance. The formula for $d(t)$ is based on the Sharpe & DeMichele equation (Rueda et al., 1990) parameterized for *Culex* with laboratory data by (Gong et al., 2011) but estimated for *Aedes* here, for which A is the development rate assuming no temperature inactivation of an enzyme critical for development; HA is the enthalpy of activation of the reaction that is catalyzed by the enzyme(cal $mol^{-}1$); HH is the enthalpy change associated with high temperature inactivation of the enzyme(cal $mol^{-}1$); K is the air temperature in Kelvin units; TH is the temperature where 50% of the enzyme is inactivated by high temperature. μ_{01} (μ_{02}) is the baseline mortality rate; T_{01} (T_{02}) is the optimal temperature for survival; v_1 (v_2) is the variance; $T(t)$ is the temperature at day t. Parameter definitions are shown in Table 2. Here, the birth rate of the immature is dependent on W, which can represent the environmental capacity, so we assume that density dependent factors are implicit in the birth rate and density-dependent competition induced death for the immature stage is not considered.

In many previous studies on the effects of temperature on mosquito abundance or of the transmission of mosquito-borne diseases, the temperature $T(t)$ is usually the mean temperature at day t. However, temperature may vary markedly within a day. The impact of daily temperature fluctuations on dengue virus transmission has been the subject of a study which revealed the importance of considering short-term temperature variations when studying dengue virus transmission (Lambrechts et al., 2011). So, in order to take the daily temperature variations into consideration, we put the diurnal temperature range (DTR) into the model as shown in (Lambrechts et al., 2011). Let x be the daily mean temperature and y be the daily DTR, assume that there is a sinusoidal hourly temperature variation between the two extremes $(x \pm y/2)$ within a period of 24 hours, and we take 48 time points in the 24 hours with 30-min intervals. The temperature on the time t_i in one day can be written as T_{t_i}.
$T_{t_i} = y\sin((t_i - 6)\pi/12)/2 + x, t_i = 0.5, 1, 1.5, \ldots, 24, i = 1, 2, \ldots, 48$. Then the daily variation of the temperature dependent parameters can be taken into consideration.

2.2. Data

2.2.1. Study area

Guangzhou is the capital of Guangdong Province in southern China which is adjacent to Hong Kong, Taiwan and southeast Asia. Guangzhou is also the largest city in Guangdong province which consists of 10 districts and 2 satellite cities. It has a humid subtropical climate with an average annual temperature of 21.9°C and the annual average rainfall ranges from 1370-2353 mm (Shen et al., 2015).

2.2.2. Weather data

The temperature and precipitation data for Guangzhou in 2014 and 2015 were obtained from a historical weather website (http: //weather.org/weatherorg_records_and_averages.htm). Also, temperature data from three districts of

Guangzhou, including Fanyu, Huadu and Zengcheng, were obtained from the China weather network, for the whole year of 2014. The temperature data include the daily maximum and minimum temperatures, so the temperature at any time within one day can be calculated by the daily mean temperature and the DTR through assuming that there is a sinusoidal hourly temperature variation between the two extremes.

2.2.3. Mosquito density

Dengue is a notifiable infectious disease in China and the dominant transmission vector in Guangzhou city is *Ae.albopictus* (Luo et al., 2012). So, as the Breteau index (BI) is the common index for *Aedes* density surveillance, the conventional surveillance method has been used systematically in Guangzhou since 2002 (Shen et al., 2015). Specifically, for each district in the city, one to three streets were selected as the BI monitoring points and containers were checked in at least 50 houses every day. BI is calculated according to the number of positive containers which contain mosquito eggs or larvae per 100 houses inspected. The mosquito surveillance data BI of the 12 districts in Guangzhou were reported almost daily by the Guangzhou CDC from September 22 to October 30, in 2014. The daily mean BIs for Guangzhou and three districts in this period are shown in Table 3. In addition, the BI in 2015 was also reported by Guangzhou CDC in the middle of March and April, and every week between July 6 and December 29.

2.3. Parameter estimation

The BI data represent only the pattern of the immature abundances and so the real numbers of immatures and adults cannot be estimated from our data. Therefore, in this analysis more concern is placed on the pattern of the immatures and adults which can describe the extent of the variation in the abundances of mosquitoes in Guangzhou. Because of this, we fitted the model to the 2014 and 2015 BI data by the least squares method. Because low temperatures and short photo periods can lead to diapause of the mosquito, we assume that the immatures remain in that stage and the adults die from December to February (Lončarić et al., 2013). So, our simulations begin from March in 2014 and with initial values $(2, 0, 0)$. Here, in order to estimate the parameters without estimating the initial values and to reduce the number of parameters needed to be estimated, we chose the initial value of immatures to be similar to the initial data of 2015. The BI data for Zengcheng, Fanyu and Huadu were used for model validation.

3. Results

3.1. Data analysis

In order to facilitate interpretation of the data and discussion of the paper's results, we first simply compare and analyze the weather data and the BI data. The mean of the daily maximum and minimum temperatures of Guangzhou and the three districts are shown in Table 4. It indicates that the mean of the daily maximum and minimum temperatures in 2015 were higher than those in 2014. The daily mean temperature for each month of Guangzhou from March to November in 2014 and 2015 are shown in Fig.1(a). It follows from this figure that the daily mean temperature of Guangzhou from March to November is between about 18°C and 30°C and the hottest months are from June to August. Besides, the difference between the daily mean temperatures for each month in 2014 and those in 2015 are also shown in Fig.1(b), which indicates that the temperatures of April, July, August, September and October in 2014 were higher than those in 2015. Fig.2 shows the DTR of each month in 2014 and 2015. It indicates that the DTR in Guangzhou ranges from about 6 to 10. In 2014, the DTRs of months from July to October were larger than 9 and in 2015 DTRs of April, August, September and October were bigger than 9. Also, the DTR in March was the lowest in both 2014 and 2015.

The daily mean precipitations for each month in Guangzhou from March to November in 2014 and 2015 are shown in Fig.3(a). The data indicate that the months with the most rainfall are May, June, July and August. Also, the difference between the daily mean precipitations for each month in 2014 and those in 2015 are shown in Fig.3(b). It follows from Fig.3(b) that the precipitations in

May, July and October in 2014 were lower than those in 2015 and precipitations in the other months in 2014 were higher. Moreover, the total precipitation in these nine months of 2014 and 2015 were calculated to be 1567.2 and 1736, which revealed that the total precipitation in 2015 was larger than that in 2014.

The mean of the BI data in the 12 districts in 2014 and the data in 2015 are shown in Fig. 4. The BI data show that the abundance of mosquitoes in 2015 was much lower than in 2014.

3.2. Results of Parameter estimation

The results of parameter estimation are shown in Table 2. Also, Fig.4 shows the goodness of the fit, in which the cycles represent the BI data and the lines show the simulation result with estimated parameters. From Fig.4 we can see that the correspondence between the simulation result and the data is good. Fig.5 shows the data and simulation results for Zengcheng, Fanyu and Huadu. The red lines represent the simulation results under the estimated parameters with Guangzhou precipitation data and temperature data for the three districts, respectively. It indicates that the simulation results for Zengcheng and Huadu fit the data well. However, the simulation results for Fanyu are a little higher than the data, which may be caused by the precipitation or the insect control measures carried out by the local government.

Fig.6 shows the time varying parameters including (a) the development rate, (b) the immature death rate and (c) the adult death rate. Fig.6 indicates that these parameters oscillate with the temperature fluctuations. Specifically, the development rate increases with increasing temperature, so that it reaches a peak in summer. Moreover, the simulation results show that when the temperature is high, the development time of the immatures is about 5 days, while when the temperature is low the development rate may be a few dozen days. Moreover, the death rates of the immatures and the adults are nonlinear functions of the temperature. According to the parameter estimation results, we obtained optimal survival temperatures for the immatures and adults of 16 and 21, respectively, as shown in Table 2. It follows from Fig.6(b) and (c) that the mortality rate of the immatures reach its maximum in summer. Also, it follows from Fig.6(c) that the mortality rate of the adults reaches maxima in summer and winter. Therefore, high temperatures in summer lead to high development and mortality rates. Moreover, the egg laying rate is a function of the precipitation. So, due to the high precipitation from May to August, the egg laying rate is also very high in summer as shown in Fig.7. It also indicates that the egg laying rate fluctuates between 3.9 and 5.4.

In order to take the diurnal variation of the temperature into consideration, we assume that there is a sinusoidal hourly temperature variation between the daily maximum and minimum temperatures. So, effects of the DTR and the daily mean temperature on the development rate, and mortality rates can be obtained as shown in Fig.8. It follows from Fig.8(a) that the daily mean temperature affects the development rate greatly and the DTR also affects the development slightly. Increasing the daily mean temperature can lead to an increase of the development rate while increasing the DTR can lead to a decrease of the development rate. In Fig.8(b) and (c), the mortality rates of the immatures and the adults show a nonlinear dependence on the daily mean temperature and the DTR. The mortality rates of both immatures and adults increase as the daily mean temperature increases when the mean temperature is above the optimal survival temperature (16 for the immature and 21 for the adult), and they decrease as the mean temperature increases when it is below the optimal survival temperature. Besides, the mortality rates increase as the DTR increases, and the variation is greater when the mean temperature is near the optimal survival temperature.

3.3. Effects of climatic changes

From Fig. 6, it is clear that the development and mortality rates of the immatures and adults reach their maxima in summer. Also, the immature development rate has a positive relationship with the abundance of mosquitoes, while the mortality rate has a negative relationship with the abundance of mosquitoes. To investigate the influence of changing the daily mean temperature on the population growth of mosquitoes, we simulated the model under certain daily mean temperature and precipitation conditions for 30 days and calculate the difference between the end value and the initial value for the immatures, which can represent the population growth of the mosquitoes. Positive values mean increasing and negative values mean decreasing mosquito abundances. Fig. 9 shows the contour plot of the difference between the end value and the initial value for the immatures with respect to the daily mean temperature and precipitation. The DTRs in simulations were chosen to be 10 (a), 8 (b) and 6 (c) which are common values for Guangzhou (see Fig.2). It follows from Fig.9 that the optimal temperature for the population growth of mosquitoes is the maximum value. Besides, temperature only leads to a positive population growth of mosquitoes if the temperature is higher than 28(a), 29(b) and 30(c), when the precipitation is larger than 4. So, the number of mosquitoes begins to decrease, when the daily mean temperature is lower than these threshold values. Moreover, the threshold temperature for the population growth of mosquitoes and the net growth of mosquitoes within 30 days increase as the DTR decreases as shown in Fig.9. From Fig.9(b) and (c), it is clear that when the temperature is lower than 27, increasing temperature may first lead to a decrease and then an increase of the population growth of mosquitoes. Furthermore, this figure also reveals that even if the daily mean temperature is very high, the number of mosquitoes may also decrease when the precipitation is very low. These results explain why the number of mosquitoes decreases in March and April and why the peak of mosquitoes always appears in late September in Guangzhou. Effects of increasing the daily mean precipitation on the population growth of mosquitoes can also be obtained from Fig.9. In all of the three figures, the higher the daily mean precipitation, the larger the number of immatures. Also, the effect of increasing precipitation on the population growth of mosquitoes is obvious when the temperature is very high.

However, the above result was obtained when the temperature and precipitation were not changed with time. Taking seasonal changes into account, a high total precipitation may not always lead to a large number of mosquitoes, although the egg laying rate is a monotonic function of the precipitation. Actually, according to the data, we found that the daily mean maximum and minimum temperatures and the total precipitation for 2015 are all higher than those of 2014. However, the BI of 2015 is less than that of 2014, indicating that high temperatures and precipitation may not always cause a large number of mosquitoes. To establish what accounts for the large number of mosquitoes in 2014, we conducted two experiments as follows: (1) a simulation of our model with the temperature of 2015 and precipitation of 2014 as shown in Fig.10(a); (2) a simulation of the model with the temperature of 2014 and precipitation of 2015 as shown in Fig.10(b). Comparing Fig.10 with Fig.4, we can see that these two results are all lower than the actual case in 2014. This indicates that distributions of both the temperature and the precipitation are key factors which led to the large number of mosquitoes in 2014. In particular, Fig.10(b) shows a large decline of the immatures' peak compared with that in Fig.4, which reveals that the distribution of precipitation is the main reason for the large abundance of mosquitoes in 2014.

To show the effects of climatic changes on the abundance of mosquitoes more clearly, we investigated the effects of increasing the daily mean temperature or precipitation for each month on the peak value of the immatures as shown in Fig.11. Fig.11(a) was obtained by simulation based on the temperatures for 2014 and Fig.11(c) was obtained by simulation based on the temperatures for 2015. Cycles of different colour show the peak value of each simulation by increasing the daily mean temperature from the base line value (the data) to the base line value plus 3, with interval 0.3. The daily mean temperature of only one month is increased for every simulation and we consider 9 months from March to November. It follows from these two figures that increasing the monthly mean temperature can lead to an increase of the peak value except in April 2014. As shown in 11(b) increasing the temperature in April 2014 has a nonlinear relationship on the peak value of the immatures. This may be because the mean temperature and the DTR in April 2014 were 23.3 and 6.7, respectively, which are similar to the case in Fig.11(c). Moreover, increasing the temperature in June, July and August are the most effective as this period is when temperatures and precipitation are highest.

However, effects of increasing the mean temperature of the same month in 2014 and 2015 were not the same, especially in March, April and May.

Fig.12 shows the effects of varying the daily mean precipitation for every month on the peak value of the immatures. Fig.12(a) and (b) were obtained by simulation based on the precipitation and the temperature in 2014 (a) and 2015 (b). Fig.12(c) and (d) were obtained by simulation based on the precipitation of 2015 and the temperature of 2014 (c) and 2015 (d). Cycles of different colour show the peak value of each simulation by increasing the daily mean precipitation from the base line value (the data) to 10 plus the base line value, with interval 1. Also, the daily mean precipitation of only one month is increased for every simulation and we considered 9 months from March to November. It follows from these two figures that little increases of the daily mean precipitation in one month can lead to a large increase of the peak value. Also, the effects of increasing precipitation in different months are not the same. Comparing Fig.12(a)-(b) and (c)-(d), we find that effects of increasing daily mean precipitation in every month are similar in Fig.12(a) and (b), and in Fig.12(c) and (d). That is to say, effects of increasing the daily mean precipitation of one month mainly depend on the distribution of the precipitation during the whole year. Furthermore, it indicates that the distribution of temperature has little influence on effects of increasing precipitation in different months, but it has great influence on the peak value. Based on the precipitation of 2014, increasing the daily mean precipitation in March, April, June, July, September and October have a large impact on the peak value for the immatures. Increasing the daily mean precipitation for May and August are also influential but the effects are relatively weak. However, based on the precipitation of 2015, increasing the daily mean precipitation for March, April, July, August, September and October are very effective, but the effect of increasing that of June is relative weak. In particular, increasing the daily mean precipitation for May has almost no effect on the peak value for the immatures. However, from Fig.3(b) we can see that the precipitation of May 2015 is much larger than that in 2014. This may explain why the BI of 2015 is less than that of 2014, although the precipitation of

2015 is larger than that of 2014.

3.4. Effects of intervention

The most common interventions in Guangzhou were clearing water and spraying insecticide. Clearing water reduces the immature abundance and water levels, thereby reducing adult abundance. Spraying of insecticide decreases the abundance of adults almost instantly. In order to analyze the effects of these two interventions, we investigated the peak value for the immatures under different control schemes. Effects of interventions on the reduction of the adults were similar, so these are not shown here.

To study effects of control measures and the optimal control time, we considered the effects of control in different months on the peak number for immatures as shown in Fig.13. Control measures are conducted once a week and last for one month in each simulation. Fig.13(a) shows the effects of clearing water and Fig.13(b) shows effects of spraying of insecticide on the reduction of the immature peak value. Obviously, these two figures show that the higher the clearing rate or the killing rate the more effective the result. Moreover, spraying of insecticide is more effective than clearing water if the control measures are conducted between April and August. Specifically, when the clearing rate is 0.3 the immature peak value can be reduced to about 10, while this can be also reached if the killing rate is 0.2.

Fig.13(a) also indicates that clearing water in March is the most effective measure to reduce the immature peak number. However, implementing the control measures in October has no effect on reducing the immature peak number because the peak time is in September. It follows from Fig.13(b), that controlling adult mosquitoes between April and August is the most effective measure. However, it is not so effective in March, probably because there are few adult mosquitoes in March.

4. Discussion

This paper examines the effect of climatic variation on the number of mosquitoes and further explores the effectiveness of the most common interventions: spraying of insecticide and clearing water to reduce the number of immatures and minimizing the extent of mosquito breeding grounds. One of the main focuses of this paper is on the reason why the abundance of mosquitoes was so large in 2014 and further to give some indications of the effects of climate on the population growth of mosquitoes. According to the results of some biological experiments (Carrington et al., 2013), there is a negative impact of large DTR on mosquito biology. So, we took daily temperature fluctuations into consideration in this paper. We initially fitted the model to the real data for 2014 and 2015 and validated the model using data from three districts in Guangzhou. With the estimated parameter values, we analyzed the time varying parameters and compared simulation results to study what led to the large number of mosquitoes in 2014. In addition, effects of increasing the daily mean temperature and precipitation were analyzed.

Results of parameter estimations indicated that the development and mortality rates of the immatures and adults oscillate with the temperature fluctuations frequently. Specifically, the development time of the immatures is about 5 days in summer which is consistent with the result in (Gong et al., 2011) and it increases with decreasing temperature. The mortality rate of the adults reached maxima in summer and winter which led to a complex relationship between the abundance of mosquitoes and the temperature. Effects of varying the daily mean temperature and the DTR on these parameters are also shown in Fig.8 which indicated that the development rate and the death rates increase as the DTR increases and effects of varying the mean temperature also vary as the DTR varies. Therefore, these parameters may have large and complex variations within one day and so cannot be neglected.

We have data on the mean temperatures and the DTR for every month in 2014 and 2015. Also, the daily mean precipitation for each month can be obtained as shown in Fig.3(b). Then, comparing the data of 2014 with those for 2015, we found that the mean temperature and the total precipitation for 2015 were larger than those of 2014, while the BI of 2015 was less than that of 2014. So, more precipitation does not necessarily lead to more mosquitoes. Similarly high mean temperatures do not always mean more mosquitoes, providing the rationale for the analysis of the reason for the large abundance of mosquitoes in 2014. Our results as shown in Fig.10 indicated that the large amount of mosquitoes in 2014 was mainly caused by the distribution of precipitation, which is consistent with the results in a previous paper (Cheng et al., 2016).

To make the relationship between the temperature, precipitation and the abundance of mosquitoes comprehensive and clear, effects of precipitation and temperature on the population growth of mosquitoes were also analyzed as shown in Fig.9. The results indicated that increasing temperature may have a positive or negative effect on the population growth of mosquitoes. This may be a reason why some studies found a negative association of dengue incidence with temperature (Wu et al., 2007) and some showed a positive correlation between dengue incidence and temperature (Lu et al., 2009). Moreover, in Guangzhou, the temperature in summer, when the daily mean temperature is around 30°C , is very beneficial for the population growth of mosquitoes and temperature increases may thus have a large effect on the abundance of mosquitoes as shown in Fig.9 and Fig.11. Besides, our results also showed that a large DTR can reduce the population growth of mosquitoes. This also agrees with the results of biological experiments (Carrington et al., 2013).

Fig.9 also indicates that increasing precipitation has a positive effect on the population growth of mosquitoes. However, effects of increasing precipitation also depend on the daily mean temperature and the DTR. As shown in Fig.12, effects of increasing precipitation in each month is very different in the case of 2014 compared with in 2015. In other words, the annual rainfall and temperature distribution determines the impact of the monthly rainfall on the number of mosquitoes. So our results show that there is no simple rule to compare the effects of precipitation and temperature, because their effects are interdependent.

In this paper, the effectiveness of government control measures against mosquitoes in Guangzhou, which are mainly spraying of insecticide and clearing water to reduce the immatures and minimize the breeding grounds, were also analyzed as shown in Fig.13. It reveals that killing adult mosquitoes and clearing water are effective measures and spraying of insecticide from April to August is more effective than clearing water. Also, effects of these two measures are different according to their implementation times. It is better to clear water early and kill the adults between April and August, in the case of limited resources.

Several studies have suggested positive associations between dengue and the abundance of mosquitoes. So, further development of the model will incorporate the transmission of dengue fever to investigate effects of mosquito abundance on outbreaks of the disease and effects of climatic variability on the incidence of dengue fever. In addition, this model can also be used to predict risk factors for other vector-borne diseases.

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Table 1: Definitions of the parameters used in the model

Parameter	Definition
$b(t)$	the egg laying rate
$d(t)$	the development rate of immatures
$\mu_1(t)$	the daily mortality rate of immatures
$\mu_2(t)$	the daily mortality rate of adults
p	the diapausing rate
$\lambda(t)$	the total daily precipitation

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Table 2: Definitions of the parameters used in the model

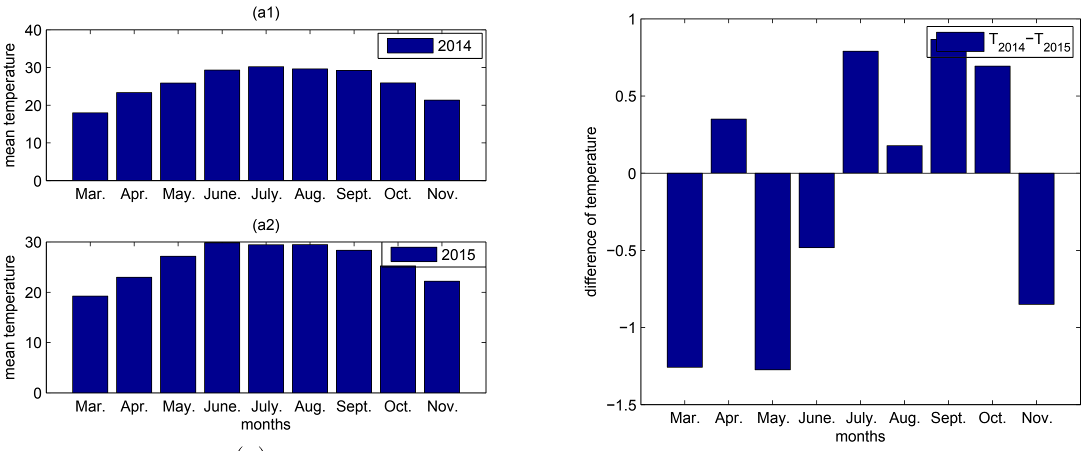
Parameter	Definition (Units)	Value	References
b_0	the baseline egg laying rate	2.4337	estimated
$E_{\max}$	the maximum egg laying rate above baseline	2.9147	estimated
E_{mean}	the value at which the moisture index produces 50% of E_{max}	0.0024	estimated
E_{var}	the variance	4.0471	estimated
A	the development rate assuming no temperature inactivation of the critical enzyme	0.1508	estimated
HA	the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal mol^-1)	39949.6	estimated
HH	the enthalpy change associated with high temperature inactivation of the enzyme (cal mol^-1)	28007.4	estimated
K	the air temperature in Kelvin units	273.15	(Gong et al., 2011)
TH	the temperature where 50% of the enzyme is inactivated by high temperature	298.8704	estimated
μ_{01}	the baseline mortality rate of immatures	0.9514	estimated
μ_{02}	the baseline mortality rate of adults	0.5943	estimated
T_{01}	the optimal temperature for survival of the immature	16.0427	estimated
v_1	the variance for immatures	6.2841	estimated
T_{02}	the optimal temperature for survival of the adults	21.0372	estimated
v_2	the variance for the adults	13.4776	estimated
δ	evaporation rate	0.6094	estimated

Table 3: Mean values of BI for each district.

Area	$meanBI$
Guangzhou	14.8912
Zengcheng	15.2537
Fanyu	22.5935
Huadu	24.1395

Table 4: Mean of the maximum and minimum temperatures for each area from March to November.

Area	T_M	T_m
Guangzhou (2014)	30.0364	21.7091
Guangzhou (2015)	30.0655	21.9018
Zengcheng	29.6509	21.9491
Fanyu	30.2982	23.2727
Huadu	29.9273	22.6764



(a) (b)

Fig. 1: (a) The monthly mean temperatures at Guangzhou from March to November 2014(a1) and 2015(a2). (b) The difference between the monthly mean temperatures in 2014 and those in 2015 from March to November.

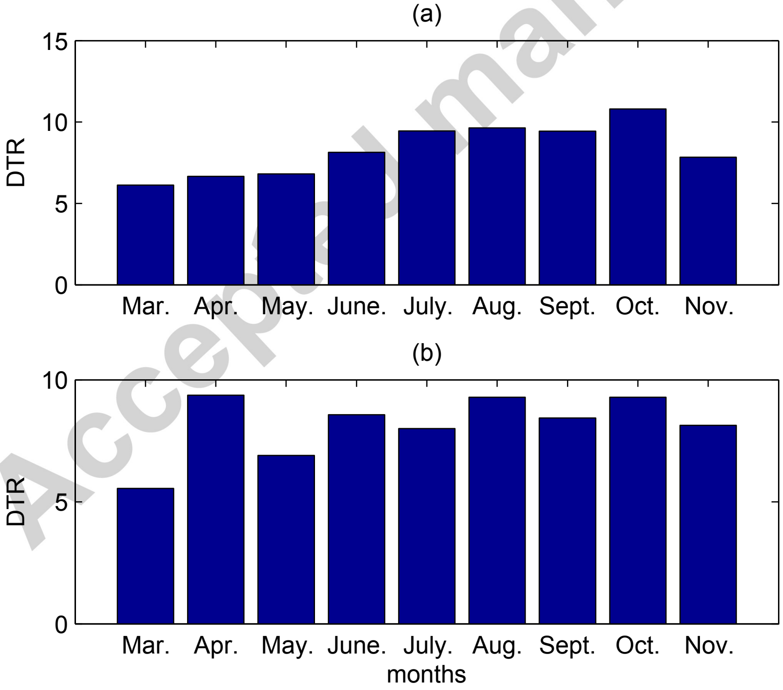
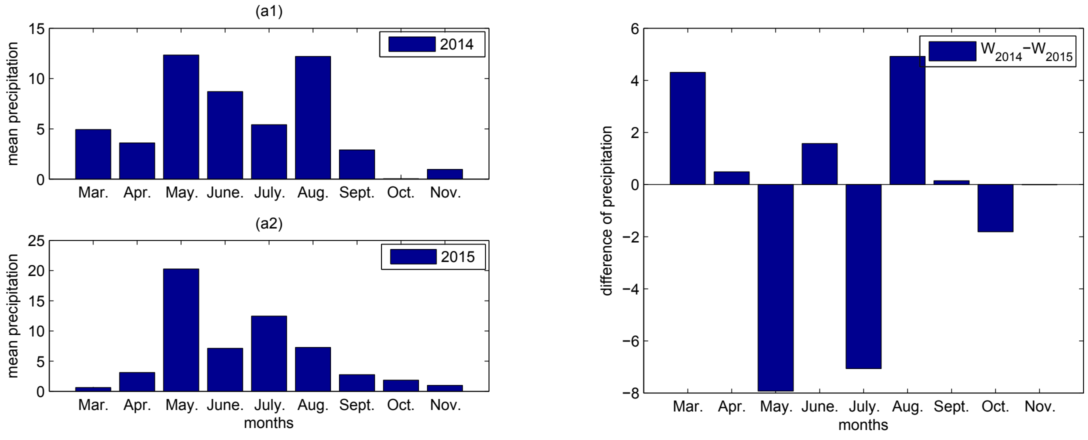


Fig. 2: The monthly mean DTRs at Guangzhou from March to November 2014(a) and 2015(b).



(a) (b)

Fig. 3: (a) The monthly precipitation at Guangzhou from March to November in 2014(a1) and 2015(a2). (b) The difference between the monthly precipitations in 2014 and those in 2015 from March to November.

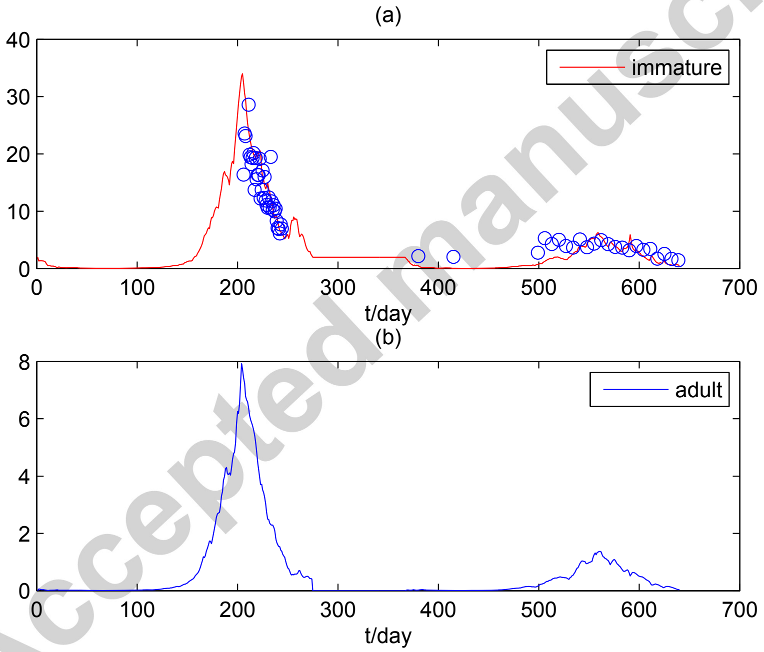


Fig. 4: Goodness fit of the model and data at Guangzhou. Circles represent the BI data, lines show the simulation results with the estimated parameters.

Fig. 5: Comparisons of the BI data and simulation results in Zengcheng, Fanyu and Huadu. Parameters values are shown in Table 2

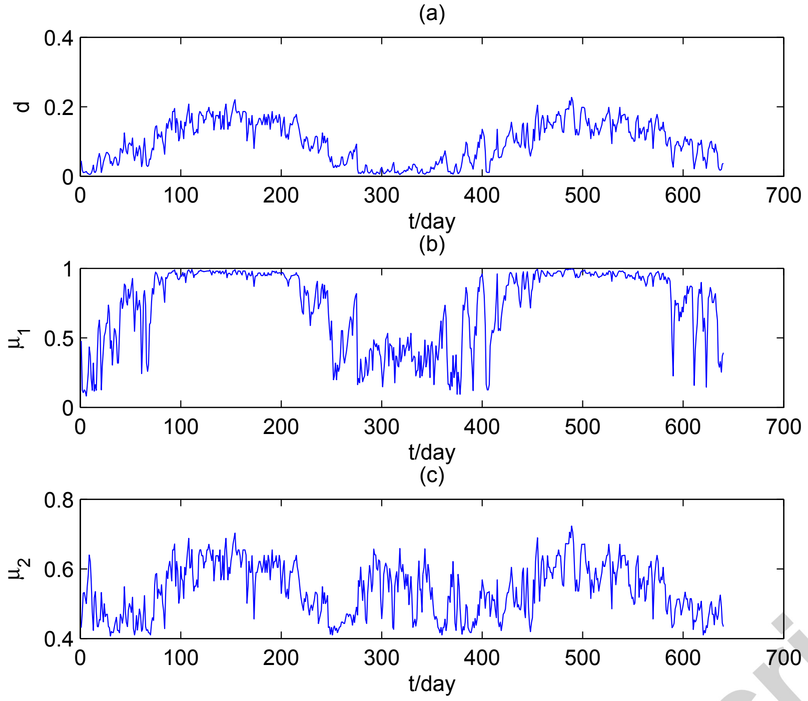


Fig. 6: Time varying parameters. (a) The development rate. (b) The death rate of the immatures. (c) The death rate of the adults. Parameter values are shown in Table 2.

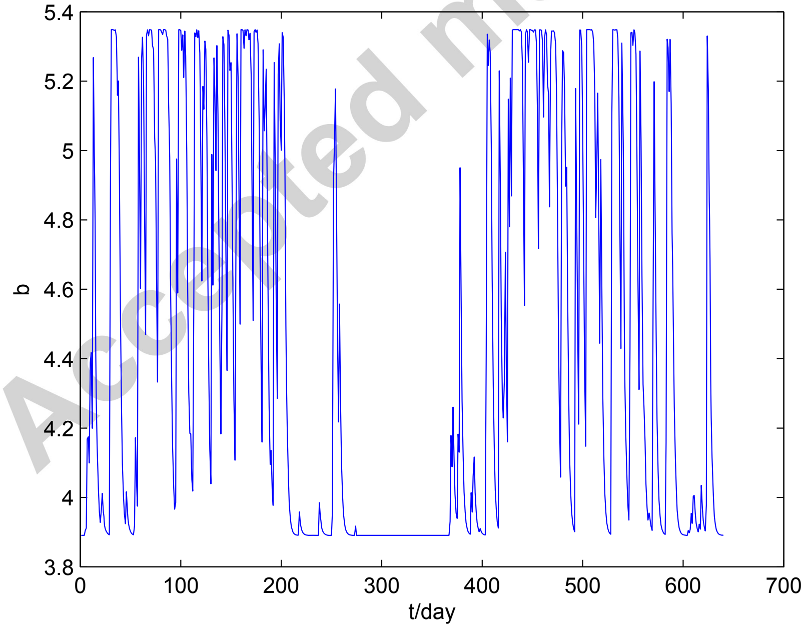
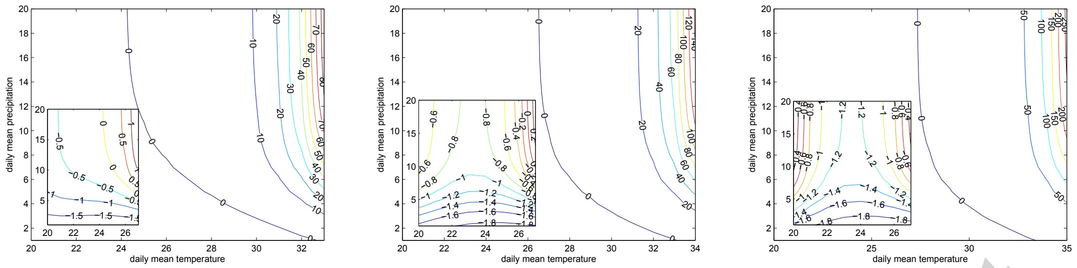


Fig. 7: The time varying egg laying rate simulated with estimated parameter values as shown in Table 2

Fig. 8: Contour plots of the development rate (a) and the survival rate of the immature (b) and adult (c) with respect to the DTR and the daily mean temperature.



(a) (b) (c)

Fig. 9: Contour plots of the difference between the end value (30 days) and the initial value for the immatures with respect to the daily mean temperature and daily mean precipitation. (a) The DTR is 10. (a) The DTR is 8. (a) The DTR is 6.

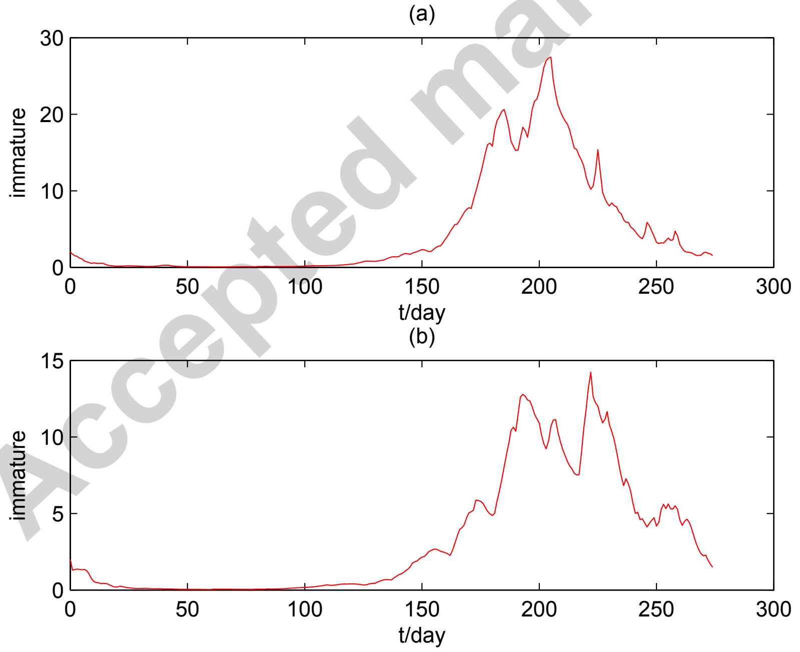


Fig. 10: (a) Simulation results with temperature of 2015 and precipitation of 2014. (b) Simulation results with temperature of 2014 and precipitation of 2015.

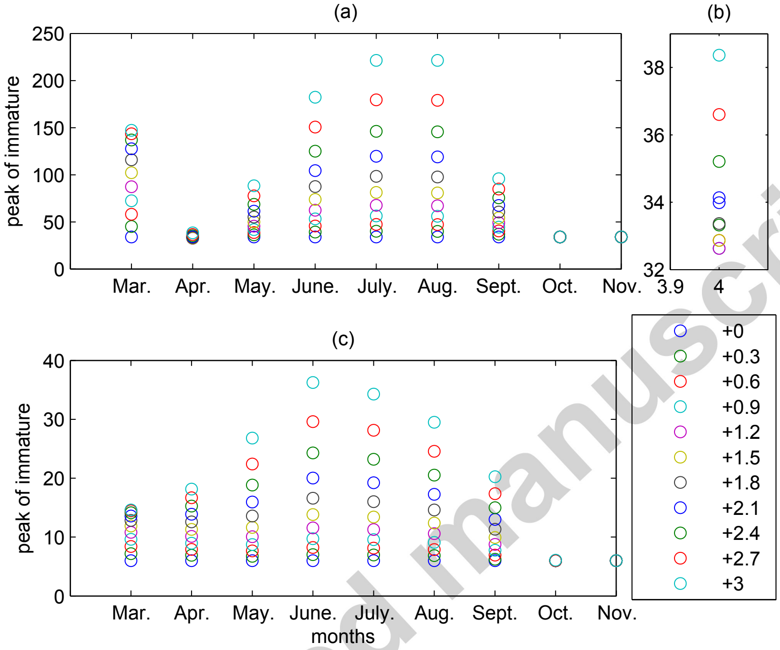


Fig. 11: Effects of increasing daily mean temperature of every month on the peak value of the immature. Circles are simulation results based on temperature and precipitation of 2014(a) and 2015(b), and the temperature change from the baseline value plus 3, with interval 0.3.

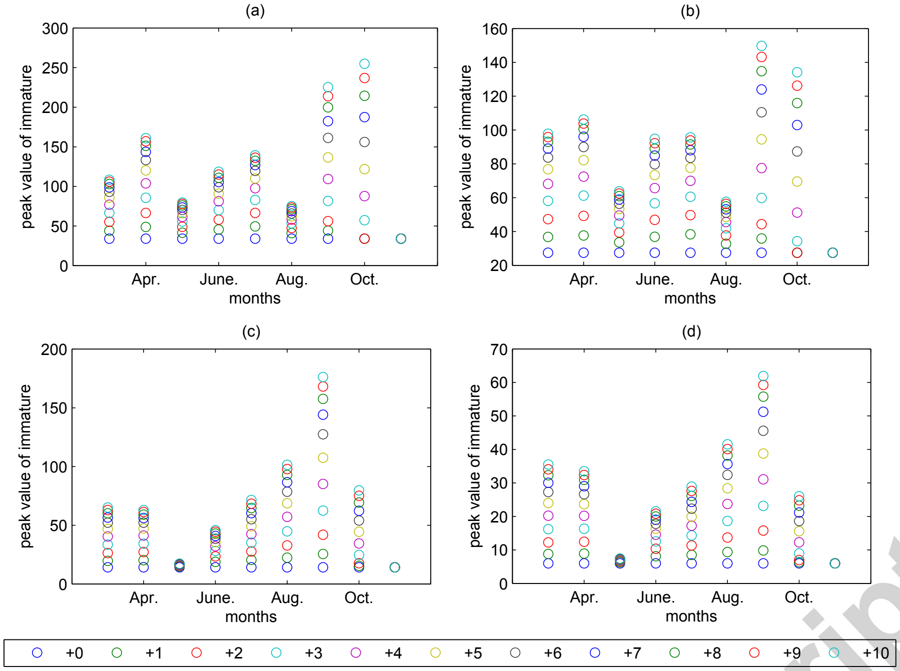


Fig. 12: Effects of increasing daily mean precipitation in every month on the number of mosquitoes. (a) Simulation results based on temperature of 2014 and precipitation of 2014. (b) Simulation results based on temperature of 2015 and precipitation of 2014. (c) Simulation results based on temperature of 2015 and precipitation of 2014. (d) Simulation results based on temperature of 2015 and precipitation of 2015. The daily mean precipitation is increased from the base line value to the base line value plus 10 with interval 1.

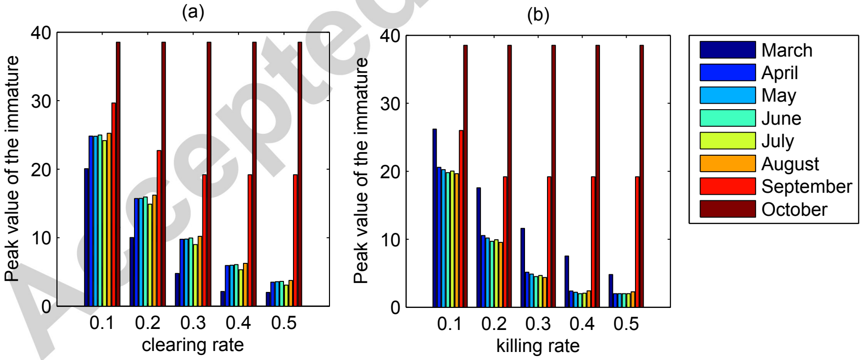


Fig. 13: Effects of interventions on the peak value for the immatures: (a) clearing water to reduce the immature mosquitoes and minimizing the extent of breeding grounds; (b) spraying of insecticide to kill adults. The measure is conducted once a week and lasts for one month in each simulation. The horizontal axis represents the clearing rate (a) and the killing rate (b) respectively, and the vertical axis represents the peak value for the immatures.